

Life cycle of *Neocalanus flemingeri* (Crustacea: Copepoda) in the Oyashio region, western subarctic Pacific, with notes on its regional variations

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ABSTRACT: The life cycle of *Neocalanus flemingeri* was investigated by analyzing population structure data collected monthly at Site H in the Oyashio region, Japan, from September 1996 through October 1997. Additional non-time-series sampling was also done at several stations covering the entire subarctic Pacific, Japan Sea and Okhotsk Sea, as a basis for regional comparison of the differing life cycles and body sizes of this species. At Site H, *N. flemingeri* spawned between January and February below 250 m depth. Copepodite Stage 1 (C1) occurred in March, and most of these had developed into C5 by early June, i.e. by the end of the phytoplankton bloom. A portion of the C4 population ceased development and remained at the thermocline to 500 m layer throughout the year. The remainder developed to C5, then migrated to 250–2000 m depth in June, and matured immediately. C6 males were present in May to July and died immediately thereafter. C6 females were observed in June to December with immature gonads and in January to February with fully mature gonads. The life cycle of *N. flemingeri* was estimated as annual for most of the population, but the small population overwintering as C4 may have a biennial life cycle. While the prosome length distributions of the C2, C3, C6 males and C6 females were unimodal, C4 and C5 exhibited bimodality. We believe this bimodality reflects sexual dimorphism for C4 and C5. Possible development sequences of each of the 2 size groups are proposed in relation to annual and biennial life cycles of *N. flemingeri*. Temporal population-structure data in other regions suggested an annual life cycle for the populations in the central-eastern subarctic Pacific, and a possible mixture of various degrees of annual/biennial life cycles for the populations in the western subarctic Pacific, Japan Sea and Okhotsk Sea. Geographical comparison of the prosome length of the C6 females between the Oyashio (Site H) and other regions indicated significantly larger specimens in the Okhotsk Sea, with smaller individuals in the eastern and part of the western subarctic Pacific. Possible causes for regional variability in life cycle and body size are discussed.

KEY WORDS: *Neocalanus flemingeri* · Life cycle · Ontogenetic vertical migration · Body size · Sexual dimorphism · Western North Pacific

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INTRODUCTION

The subarctic Pacific Ocean and adjacent Bering, Japan and Okhotsk Seas have common sets of pelagic species (cf. Zenkevitch 1963). Among the zooplankton,

copepods are an integral component. Large grazers such as *Neocalanus cristatus*, *N. plumchrus* and *Eucalanus bungii* often account for 80 to 90% of the zooplankton biomass of the surface layer (Vinogradov 1970). These large grazing copepods are known to be preyed upon by various pelagic fishes, whales and sea birds (Nemoto 1963, Fukataki 1967, 1969, Taka et al. 1982, Odate 1994, Hunt et al. 1998), and are therefore a vital link between primary production and predators in these regions.

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Neocalanus flemingeri was only recently described as a new species by Miller (1988). Before Miller's description, this species had long been confused with *N. plumchrus* because of their similar morphology. Studies have shown that *N. flemingeri* and *N. plumchrus* have dissimilar life cycles (Miller & Clemons 1988, Miller & Terazaki 1989, Tsuda et al. 1999). Ontogenetic vertical migration and the life cycle of *N. flemingeri* were first evaluated at Stn P in the eastern subarctic Pacific (Miller & Clemons 1988), and then in the Japan Sea (Miller & Terazaki 1989). According to these studies, the life cycle of *N. flemingeri* is annual in the eastern subarctic Pacific, but biennial in the Japan Sea. Recently, Tsuda et al. (1999) studied the life cycle of *N. flemingeri* in the Oyashio region, Japan, and noted the occurrence of 2 distinct size groups in Copepodite Stages 4 and 5 (C4 and C5). They interpreted the smaller size group to be the local population in the Oyashio region and the larger size group to be individuals transported from the Okhotsk Sea. From the viewpoint of ontogenetic vertical migration of *N. flemingeri* (near the surface to >1000 m depth: Miller & Clemons 1988, this study), however, the sampling by Tsuda et al. (1999) did not cover the entire depth range of *N. flemingeri*. Clearly, a more thorough collection covering its entire habitat is needed to gain a better picture of the life cycle pattern of *N. flemingeri* in the Oyashio region.

In this study, we propose an alternative life cycle of *Neocalanus flemingeri* to that hypothesized by Tsuda et al. (1999); our study is based on new year-round population data collected from the surface to ≤ 2000 m depth, and develops an alternative interpretation (sexual dimorphism) for the 2 size groups seen in the late copepodite stages. Regional variations in the life cycle and body size of *N. flemingeri* in the subarctic Pacific and its marginal seas are also discussed.

METHODS

Monthly depth-stratified sampling was done in the Oyashio region ($41^{\circ}30'$ to $42^{\circ}30'$ N latitude, $145^{\circ}00'$ to $146^{\circ}00'$ E longitude) off southeastern Hokkaido (referred to hereafter as Site H). We also obtained occasional samples from 3 additional stations in the western, 1 station in the central, and 2 stations in the eastern subarctic Pacific, 4 stations in the Japan Sea, 2 stations in the Okhotsk Sea and 1 station in the western Bering Sea (Fig. 1, Table 1). Except for the sampling in the Bering Sea (February 1993), all other samples were collected from September 1996 to October 1997.

Zooplankton were collected with a closing net (60 cm mouth diam., 100 μm mesh size; Kawamura 1968, 1989), equipped with a Rigosha flow-meter in its mouth ring and a TSK depth-distance recorder or RMD depth meter on its suspension cable. The net was towed vertically at a speed of 1 m s^{-1} , usually through 5 discrete strata: 0 (surface) to the bottom of the thermocline, the bottom of thermocline to 250, 250 to 500 m, 500 to 1000 m, and 1000 to ≤ 2000 m (Table 1). When the sampling failed to obtain a complete discrete depth series

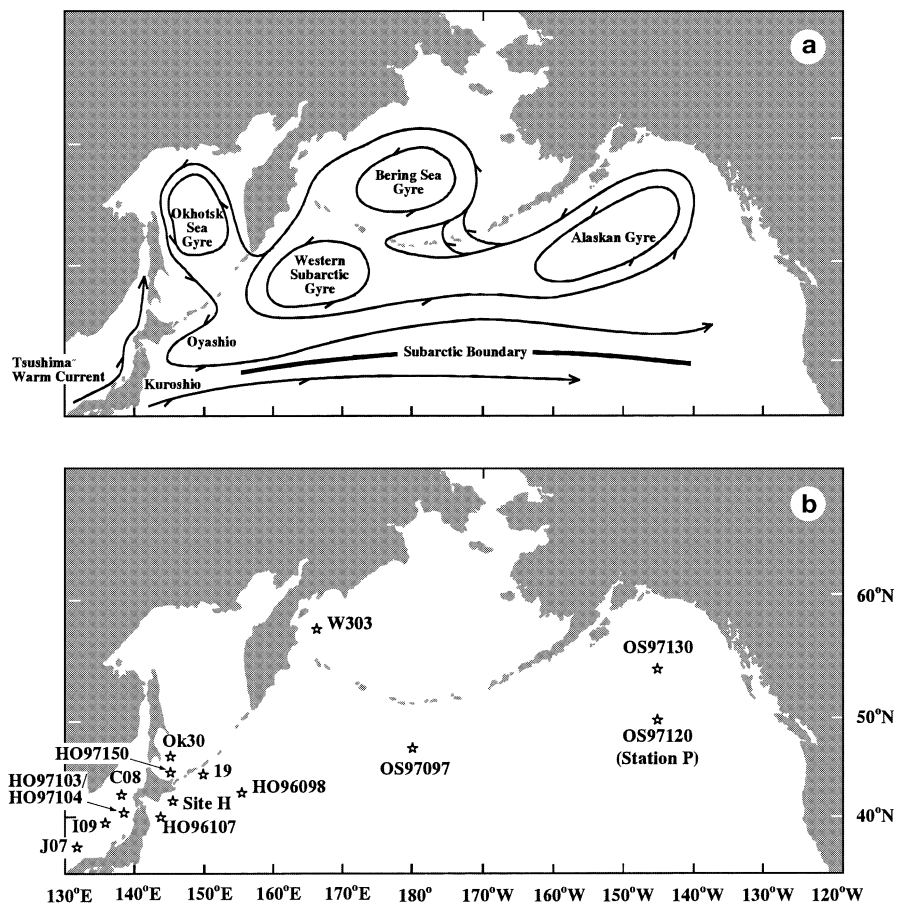


Fig. 1. (a) Current systems (redrawn from Favorite et al. 1976) and (b) sampling stations in the subarctic Pacific Ocean and its neighboring waters

during the monthly samplings, missing depth-stratum data were time-interpolated from data for the previous and subsequent sampling dates. Since the samples were obtained without standardizing the time of day, diel vertical migration of *Neocalanus flemingeri* could be a potential source of error in estimating the vertical distribution pattern of *N. flemingeri*. However, *N. flemingeri* is known to carry out little or no diel vertical migration (Mackas et al. 1993, Tsuda & Sugisaki 1994, Kobari & Ikeda unpubl. data). For the isolated samples in the Bering Sea, where specimens were used for prosome length measurements only, a WP-2 net (57 cm mouth diam., 200 µm mesh size; UNESCO 1968) was used. After collection, zooplankton samples were preserved in 5% formalin-seawater buffered with borax.

Temperature and salinity profiles were determined with a CTD system at each sampling of zooplankton. Chlorophyll *a* concentration data at Site H were supplied by H. Kasai of Hokkaido National Fisheries Research Institute.

In the laboratory, *Neocalanus flemingeri* was sorted from the zooplankton samples, then separated into 5 copepodite stages (C2 to C6) under a dissecting microscope. The C1 of *N. flemingeri* could not be distinguished from that of *N. plumchrus* because of undeveloped second maxilla and the mandibular gnathobase. C6 specimens were separated into males and females. *N. flemingeri* was distinguished from *N. plumchrus* by its smaller proportion of second maxilla to prosome (Tsuda et al. 1999), its wider tooth row on the

Table 1. Zooplankton sampling data in the subarctic Northwest (NW), Northcentral (NC) and Northeast (NE) Pacific and its neighboring waters. NT: nighttime; DT: daytime; Os: TS 'Oshoro Maru'; Ho: TS 'Hokusei Maru'; Hs: RV 'Hokushin Maru'; Hk: RV 'Hokko Maru'; Ts: RV 'Tansei Maru'; Ky: RV 'Kaiyo Maru'; WP-2: WP-2 net; G: closing type net

Area Station code	Position	Sampling date	Time	Ship	Net	Discrete sampling depth (m)
NW Pacific						
Site H						
	42° 00' N, 145° 00' E	4 Sep 1996	NT	Os	G	0–30, 30–250, 250–500, 500–1000, 1000–1800
	41° 30' N, 145° 47' E	19 Sep 1996	NT	Ho	G	0–30, 30–250, 250–500, 500–1000, 1000–1500
	41° 30' N, 145° 47' E	2 Oct 1996	DT	Ho	G	0–30, 30–250, 250–500, 500–1000, 1000–1500
	41° 30' N, 146° 00' E	8 Dec 1996	NT	Hs	G	0–80, 80–250, 250–500, 500–1000, 1000–1700
	42° 30' N, 145° 00' E	13 Jan 1997	DT	Hk	G	0–50, 10–500, 300–1700
	41° 30' N, 146° 00' E	20 Feb 1997	NT	Hs	G	0–100, 100–250, 250–500
	41° 45' N, 145° 22' E	17 Mar 1997	NT	Hk	G	0–100, 100–250, 250–500, 500–1000, 1000–2000
	41° 30' N, 145° 47' E	11 Apr 1997	NT	Ho	G	0–150, 150–250, 250–500, 500–1000, 1000–1500
	42° 01' N, 145° 21' E	7 May 1997	NT	Hk	G	0–150, 500–1000, 1000–2000
	41° 30' N, 145° 47' E	4 Jun 1997	NT	Os	G	0–80, 80–250, 250–500, 500–1000
	41° 30' N, 145° 47' E	23 Jun 1997	NT	Ho	G	0–20, 20–250, 250–500, 500–1000
	41° 30' N, 145° 47' E	2 Jul 1997	NT	Ho	G	0–40, 40–250, 250–500, 500–1000, 1000–2000
	41° 30' N, 145° 47' E	17 Aug 1997	NT	Os	G	0–80, 80–250, 250–500, 500–1000, 1000–2000
	41° 29' N, 145° 47' E	26 Aug 1997	DT	Ts	G	0–20, 20–250, 250–500, 500–1000, 1000–2000
	41° 30' N, 145° 47' E	5 Oct 1997	NT	Ho	G	0–75, 75–250, 250–500, 500–1000, 1000–2000
HO96098	42° 30' N, 155° 00' E	27 Sep 1996	NT	Ho	G	0–40, 40–250, 250–500, 500–1000, 1000–1500
HO96107	40° 32' N, 144° 29' E	3 Oct 1996	DT	Ho	G	0–30, 30–250, 250–500, 500–1000, 1000–1500
19	44° 26' N, 149° 40' E	16 Oct 1996	DT	Ky	G	0–50, 50–250, 250–500, 500–1000, 1000–2000
NC Pacific						
OS97097	47° 00' N, 180° 00' E	18 Jun 1997	NT	Os	G	0–100, 100–250, 250–500, 500–1000, 1000–2000
NE Pacific						
OS97120 (= Stn P)	50° 00' N, 145° 00' W	5 Jul 1997	NT	Os	G	0–40, 40–250, 250–500, 500–1000, 1000–2000
OS97130	55° 00' N, 145° 00' W	10 Jul 1997	NT	Os	G	0–40, 40–250, 250–500, 500–1000, 1000–2000
Bering Sea						
W303	57° 08' N, 165° 53' E	8 Feb 1993	NT	Ky	WP-2	0–500
Japan Sea						
C08	42° 30' N, 137° 30' E	11 Jan 1997	NT	Ky	G	0–100, 100–500, 500–1000, 1000–2000, 2000–3000
I09	39° 00' N, 135° 00' E	24 Jan 1997	NT	Ky	G	0–100, 100–500, 500–1000
J07	37° 00' N, 131° 30' E	26 Jan 1997	NT	Ky	G	0–200, 200–500, 500–1000, 1000–2000
HO97103	40° 48' N, 138° 19' E	19 Sep 1997	DT	Ho	G	0–100, 100–250, 250–500, 500–1000, 1000–2000
HO97104	40° 48' N, 138° 19' E	19 Sep 1997	NT	Ho	G	0–100, 100–250, 250–500, 500–1000, 1000–2000
Okhotsk Sea						
Ok30	46° 00' N, 145° 00' E	9 Nov 1996	DT	Ky	G	0–50, 50–250, 250–500, 500–1000, 1000–2000
HO97150	44° 40' N, 145° 20' E	1 Oct 1997	NT	Ho	G	0–50, 50–250, 250–500, 500–1000, 1000–2000

mandibular gnathobase for C2 to C5, its smaller head/prosome ratio for the C6 male, and its smaller width of the first urosome segment for the C6 female (Miller 1988). The sexual maturity of the C6 females was classified into the following 4 categories, based on gonad

condition: dormant, developing, actively spawning and spent, following the criteria of Miller & Clemons (1988). As an index of body size, the prosome length of specimens was measured under a dissecting microscope to the nearest 0.05 mm.

RESULTS

Hydrography

Site H

The western boundary current of the subarctic circulation in the North Pacific is called the 'Oyashio'. It flows southwestward along the Kuril Islands and reaches the east coast of northern Honshu, Japan, then turns east at about 40° N (cf. Reid 1973). During its journey, the properties of Oyashio water are modified as a result of exchange with Okhotsk Sea water, Tsugaru Warm-Current water, and Kuroshio water (Kono 1996). Because of its meandering flow pattern, isolated loops of the Kuroshio extension are often entrapped between the downstream and return flows of the Oyashio and are called 'warm-core rings'.

Site H of this study is near the southern end of the alongshore flow of the Oyashio. Over the study period, surface temperatures ranged from 2°C (March to April 1997) to 18°C (September to October 1996 and 1997) (Fig. 2). Oyashio water, characterized by salinities from 33.0 to 33.3 psu and temperatures below 3°C (Ohtani 1971), occurred in the upper 150 m from February to April 1997. After April, less saline, seasonally warmed water (possibly originating from the Okhotsk Sea; T. Kono pers. comm.) occupied the upper 50 m. Surface temperatures above 10°C were observed in September to November 1996 and in June to October 1997, when the thermocline was well established at 20 to 50 m in the water column. Effects of warm-core rings originating from the Kuroshio extension were seen in September of both 1996 and 1997, and from December 1996 to January 1997, as judged by temperature at 200 m (>4°C) and salinity in the 0 to 200 m layer (>33.5 psu). The temperature and

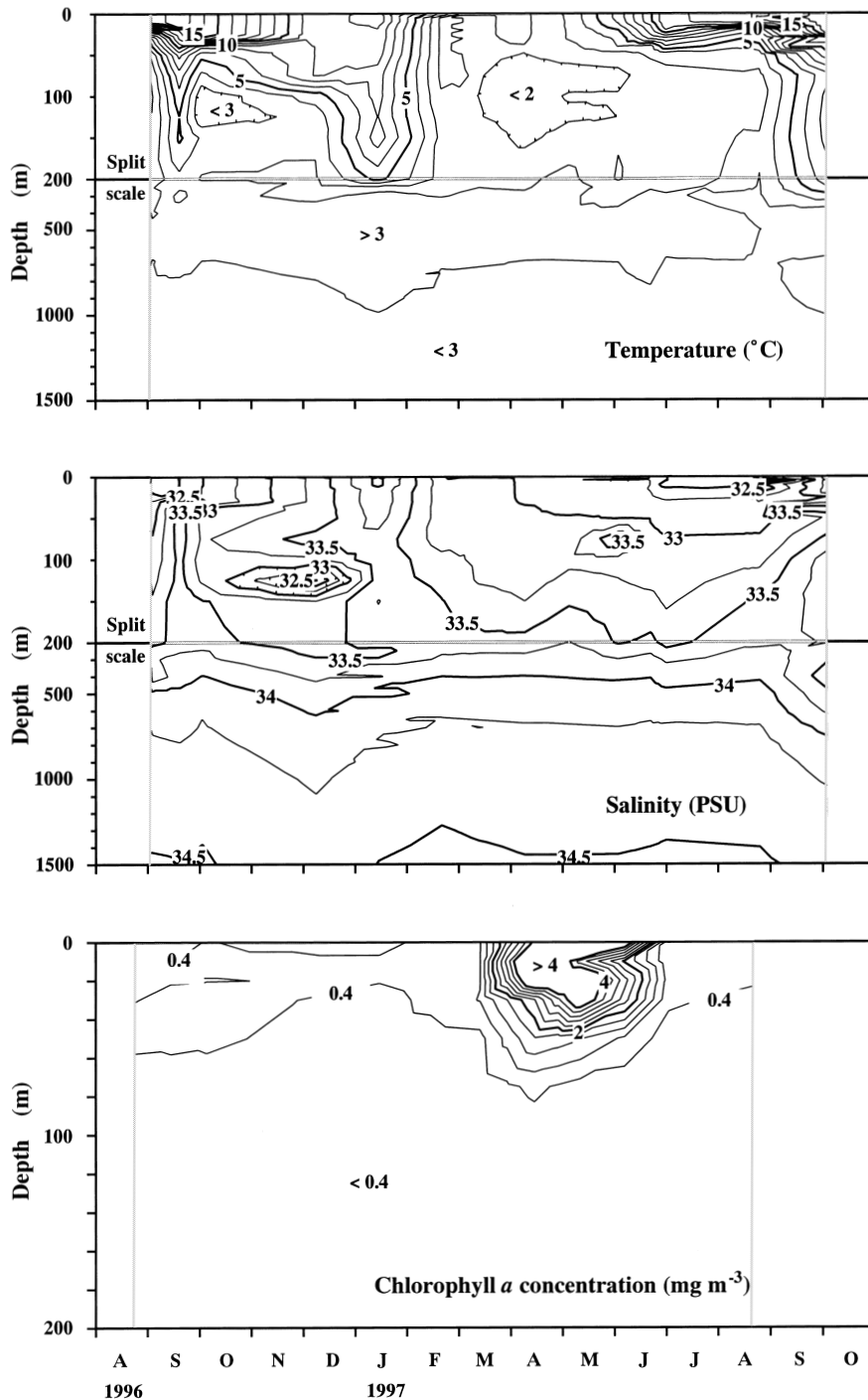


Fig. 2. Seasonal changes in vertical structures of temperature, salinity and chlorophyll *a* concentration at Site H from August 1996 to October 1997. Note that depth scale in the bottom panel is not the same as in the top 2 panels

salinity in the 200 to 1500 m layer were stable and nearly constant at 2 to 3°C and 33.5 to 34.5 psu, respectively, throughout the year.

Phytoplankton biomass estimated from chlorophyll *a* (chl *a*) content showed a marked seasonality (Fig. 2). Chl *a* at the surface was around 0.4 mg m⁻³ from August 1996 to the end of February 1997, and then increased rapidly to >9 mg m⁻³ in May 1997. During this period, concentrations above 2 mg m⁻³ extended down to 50 m. The surface chl *a* concentrations had decreased to 2 mg m⁻³ by the end of June and to 0.4 mg m⁻³ toward the end of 1997. Chl *a* was consistently as low as <0.4 mg m⁻³ below 100 m depth throughout the year.

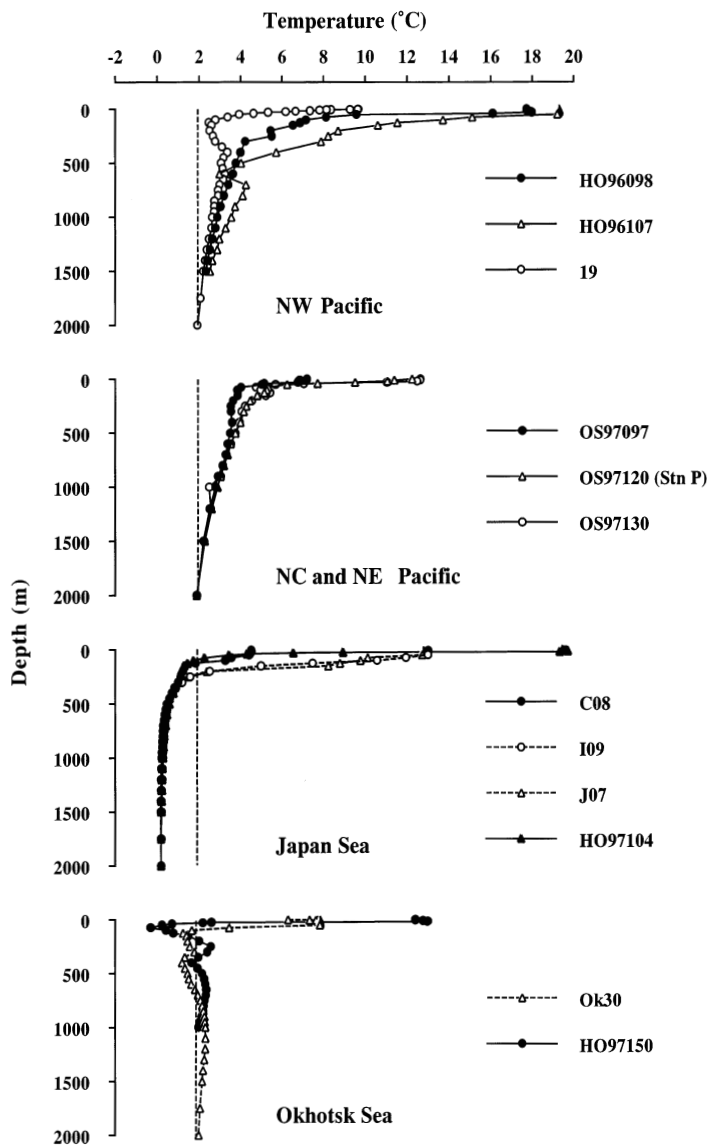


Fig. 3. Vertical structure of temperature (°C) at additional stations in Northwest (NW), Northcentral (NC) and Northeast (NE) subarctic Pacific, and in Japan and Okhotsk Seas. Vertical dashed lines (2°C) are superimposed to facilitate comparison

Other areas

At 3 stations in the western subarctic Pacific, temperatures in the top 500 m increased in the order of Stns 19, HO96098, and HO96107 (Fig. 3). Compared with Site H, the upper 500 m of Stns 19 and HO96107 were colder and warmer, respectively, and HO96098 was similar to Site H (except for higher temperatures near the surface layer). The colder temperatures at Stn 19 reflect the influence of cold Okhotsk Sea water; the warmer temperatures at HO96107 are due to the influence of the warm Kuroshio water (cf. Kono 1997, Kono & Kawasaki 1997). Temperature profiles at Stn OS97097 in the central subarctic Pacific, and Stns OS97120 (Stn P) and OS97130 in the eastern subarctic Pacific were nearly comparable to that at Site H, except that the top 500 m was slightly warmer in the latter 2 stations. Comparison of annual temperature variation in the top 500 m at Site H (Fig. 2) and at Stn P (Miller et al. 1984) showed that Site H was characterized by a wider temperature range in the surface layer (2 to 18 and 6 to 14°C for site H and Stn P, respectively) and lower temperatures in the 200 to 500 m stratum (2 to 3 and 4 to 5°C for site H and Stn P, respectively).

The thermal regimes in the marginal seas (Japan Sea and Okhotsk Sea) differed from those in the subarctic Pacific by the presence of water of near-zero temperature (Zenkevitch 1963). This very cold water is termed 'deep-water' in the Japan Sea (Nishimura 1969), and 'cold intermediate water' in the Okhotsk Sea (Kitani & Shimazaki 1972). At all 4 stations in the Japan Sea, the deep-water was below 500 m. At Stns I09 and J07 in the southern Japan Sea, water temperature in the top 300 m was higher than at Stns C08 and HO97104 in the northern Japan Sea, perhaps due to the effect of the Tsushima Warm Current (a branch of Kuroshio carrying warm water from the south, Nishimura 1969). Nishimura classified Japan Sea regions as 'subtropical', 'subarctic' and 'arctic' based on biological features. According to his classification, Stns C08 and HO97103/HO97104 in the northern Japan Sea are in the subarctic region, and Stns I09 and J07 in the southern Japan Sea are in the subtropical region. At 2 stations in the Okhotsk Sea, the 'cold intermediate water' was at 30 to 200 m depth, i.e. shallower than in the Japan Sea. This was especially evident at the southern Stn HO97150.

Population structure

Site H

Two prominent abundance peaks of the C1 of *Neocalanus plumchrus/flemingeri* were observed in March and June 1997 (Fig. 4). By tracing the abundance peaks

of *N. flemingeri* for C2 in March, C3 and C4 in April, C5 and C6 males in June, and C6 females in July, it is evident that the earlier peak of the C1 (March) consists of *N. flemingeri*. Abundance peaks of C1 to C6 all occurred within the high chl *a* period. Taking into account the sampling gap in this study (ca 1 mo), the development time from C1 to C6 is roughly estimated as 3 to 4 mo. C4 occurred throughout the year although abundance was low in September to December 1996 and May to October 1997. Although C6 males were observed only in May to July 1997, C6 females occurred throughout the year and were abundant in August to December 1996 and July to October 1997.

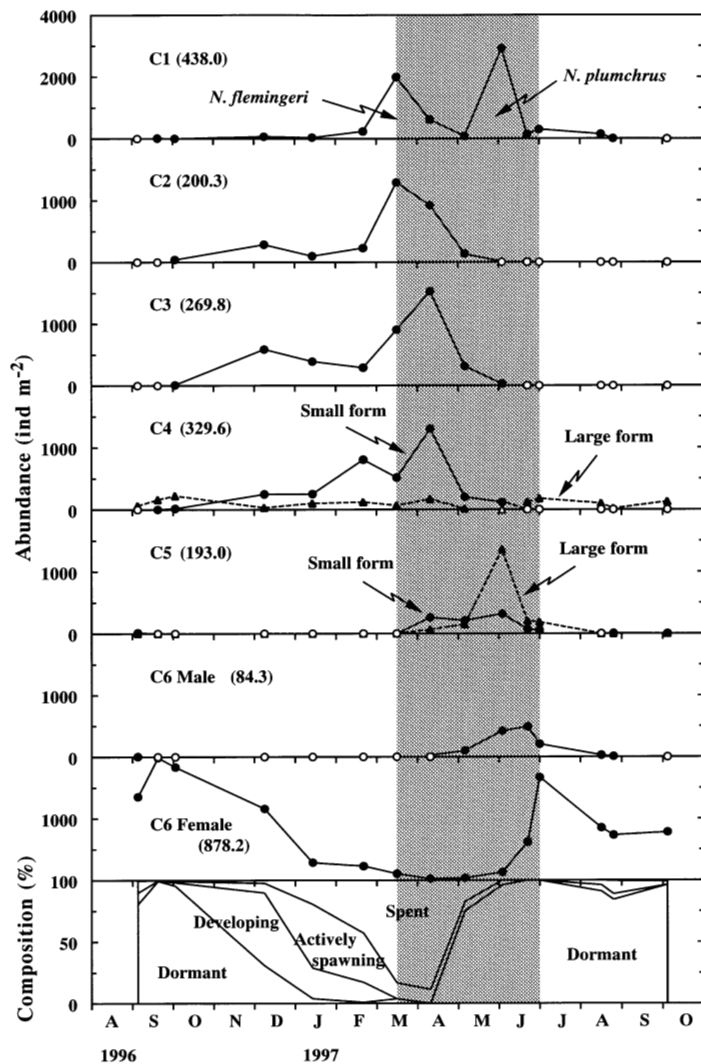


Fig. 4. *Neocalanus flemingeri*. Seasonal changes in standing stock of each development stage (C1 to C6) and composition of dormant, developing, spawning and spent specimens of C6 females at 0 to 2000 m at Site H from September 1996 to October 1997. Annual means are shown in parentheses. Shaded area: period of high chlorophyll; (●) occurrence; (○) no occurrence

The reproductive state of the C6 females varied as a function of sampling date. A large fraction of dormant specimens was observed in September to October 1996 and May to October 1997. In 1996, they were successively replaced by developing specimens in the following 2 to 3 mo. Actively spawning females were abundant from January to February 1997. Spent females were numerous in March to April 1997. Based on all these seasonal features of the population structure and maturity conditions of the females, the life cycle of most *Neocalanus flemingeri* at Site H is annual. However, a possible overwintering of a small fraction of the population as C4 copepodites molting to C5 in their second year cannot be ruled out.

Other areas

Compared with the results at Site H, population sizes (expressed as total ind. m^{-2} of C2 to C6) were significantly less in the eastern subarctic Pacific (OS97120 and OS97130), the Japan Sea (C08, I09 and J07), and the Okhotsk Sea (Ok30 and HO97150) (Table 2). On the other hand, C2 to C6 population size at the northern stations in the western (Stn 19) and central subarctic Pacific (OS97097) was much greater than that recorded at Site H.

In terms of developmental stage composition, both C4 and C6 females co-occurred in deep samples from the western subarctic Pacific, Japan Sea and Okhotsk Sea. Because the sampling season was autumn/winter, C4 in these regions were considered to be overwintering populations, as at Site H. However, the most abundant stage at all sites was C6, and C4 was not found in the central and eastern subarctic Pacific, despite similar sampling season.

Vertical distribution

Site H

C2 to C3 occurred mainly in the top 250 m from October 1996 to June 1997 (Fig. 5). A large part of the C4 population was found in the surface layer during the period of high chlorophyll (February to June 1997), and in the thermocline down to 500 m during the rest of the year. C5, which was absent from September 1996 to March 1997, occurred in the surface layer in April 1997, and sank gradually to 1000 m depth toward October 1997. All C6 males resided in the 250 to 1000 m depth layer. C6 females occurred at 500 to 2000 m in September to October 1996 and August to October 1997, during which time they were dormant; they then migrated upward and were distributed between 250 and 1000 m in March to July 1997.

Other areas

C2 to C3 were found mainly in the top 250 m at Stn 19 in the Japan Sea and Stn Ok30 in the Okhotsk Sea (Fig. 6). A large part of the C4 population was observed in the thermocline to 1000 m layer, as during summer/winter at Site H. C5 were abundant in the surface layer only in the central subarctic Pacific, and were in the thermocline to 500 m stratum at other stations: Stn 19 in the western subarctic Pacific, I09 and J07 in the Japan Sea, and HO97150 in the Okhotsk Sea. C6 males and females occurred abundantly in the 250 to 2000 m layer at all stations in the entire subarctic Pacific, Japan Sea and Okhotsk Sea. Stage-specific vertical distribution patterns were almost identical to those already described for Site H.

Table 2. *Neocalanus flemingeri*. Standing stock (ind. m^{-2} at 0 to 2000 m depth) and stage composition (%) of each development stage (C2 to C6) in the subarctic North Pacific and its neighboring waters. Standing stock and stage composition at Site H are annual means ($\pm 95\%$ CI for the former in parentheses). *0 to 1000 m depth

Area Station	Standing stock	Composition (%)				
		C2-C3	C4	C5	C6 male	C6 female
NW Pacific						
Site H	1862.5 (± 510.1)	19.2	16.1	9.3	5.4	50.0
HO96098	647.9	0.0	14.4	0.0	0.0	85.6
HO96107	418.3	0.0	10.1	0.0	1.0	88.9
19	3717.9	58.7	10.1	0.1	0.0	31.1
NC Pacific						
OS97097	4950.2	0.0	0.0	89.9	10.1	0.0
NE Pacific						
OS97120 (= Stn P)	786.6	0.0	0.0	0.0	7.8	92.2
OS97130	584.2	0.0	0.0	0.0	4.2	95.8
Japan Sea						
C08	661.7	0.0	86.7	0.0	0.0	13.3
I09	201.7*	0.0	93.3	3.3	0.0	3.3
J07	599.7	0.0	92.4	2.1	0.0	5.5
HO97103	1081.9	2.1	73.0	0.0	0.0	24.9
HO97104	1476.2	0.3	90.9	0.0	0.0	8.8
Okhotsk Sea						
Ok30	850.5	28.1	40.2	0.0	0.0	31.6
HO97150	1252.2	0.0	36.4	1.1	4.0	58.4

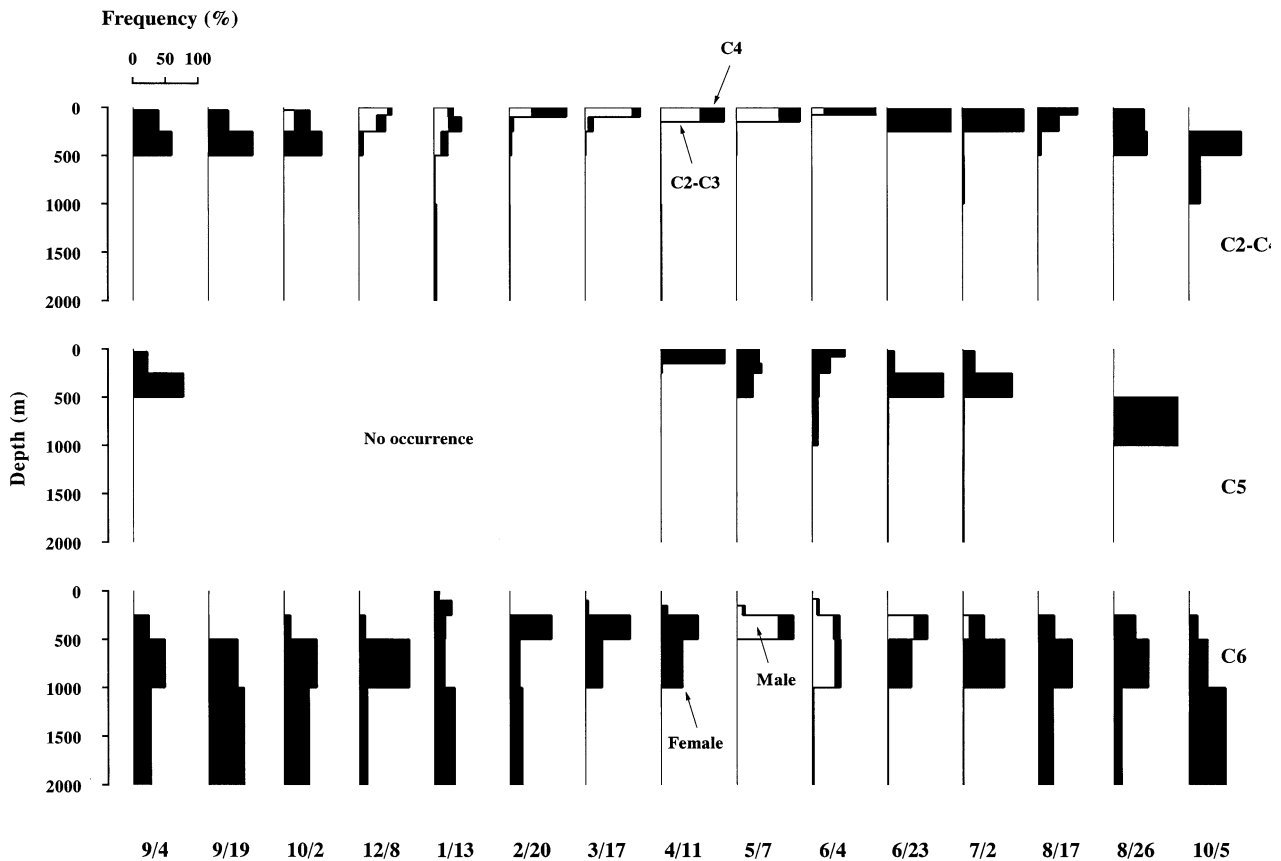


Fig. 5. *Neocalanus flemingeri*. Seasonal changes in vertical distribution of C2 to C4, C5 and C6 at Site H from September 1996 to October 1997. Date (mo/d) of sampling is shown on bottom abscissa

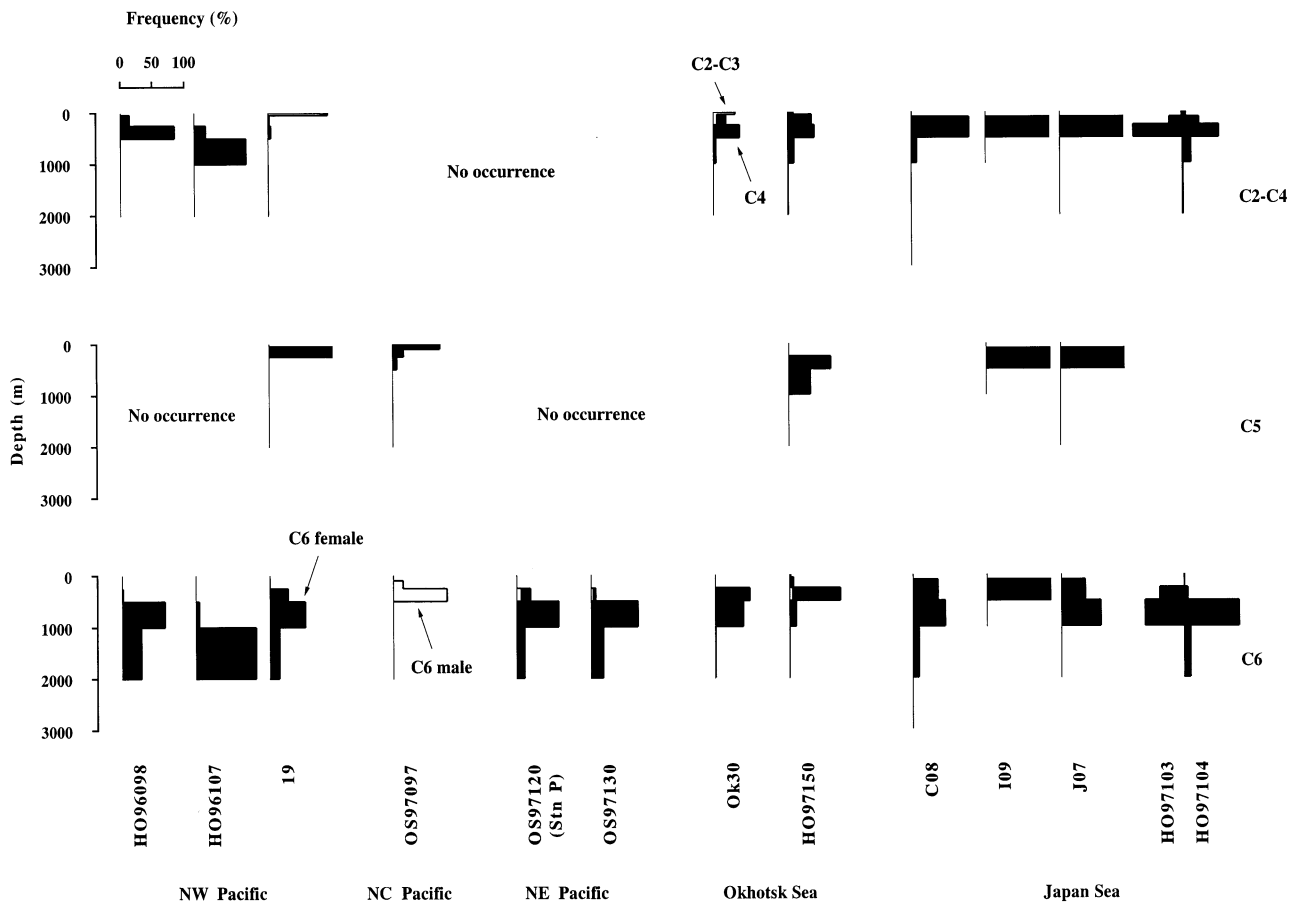


Fig. 6. *Neocalanus flemingeri*. Regional variations in vertical distribution of C2 to C4, C5 and C6 at additional stations in Northwest (NW), Northcentral (NC) and Northeast (NE) Pacific, and in Japan and Okhotsk Seas

Prosome length

Site H

Prosome length increased steadily with development from C1 to C6. However, the size distributions of prosome length were unimodal in C2, C3, C6 males and C6 females, but bimodal in C4 and C5 (Fig. 7). Large C4 was less abundant than small C4, but they nevertheless constituted nearly the entire overwintering C4 population (Fig. 4). On the other hand, large C5 were more numerous than small C5, and both occurred during the period of high chlorophyll (Fig. 4). The large-form:small-form ratio of the prosome length was 1.25:1 for C4, and 1.20:1 for C5.

Other areas

While the prosome lengths of C5, C6 males and C6 females were determined, only female C6 data were used for regional comparison, because few data were available for C5 and C6 males (Table 3). The prosome

length of C6 females was greatest in the Okhotsk Sea and smallest in the eastern and part of the western (HO96098) subarctic Pacific, with intermediate lengths in the western subarctic Pacific including Site H, and the Japan and Bering Seas (1-way ANOVA and Scheffé's *F*).

DISCUSSION

Life cycle

According to Miller & Clemons (1988), spawning of *Neocalanus flemingeri* at Stn P in the Gulf of Alaska occurs in January, and resultant offspring develop in the surface layer from February through May until they reach the pre-adult C5 stage. C5 individuals then descend from the surface layer in May/June and molt immediately to adults (C6). C6 males live for about 2 mo, and C6 females with attached spermatophores are found during June/July. Throughout the remainder of summer and autumn, the entire population is constituted of C6 females with small, immature ovaries (perhaps a diapause phase). Ovarian development be-

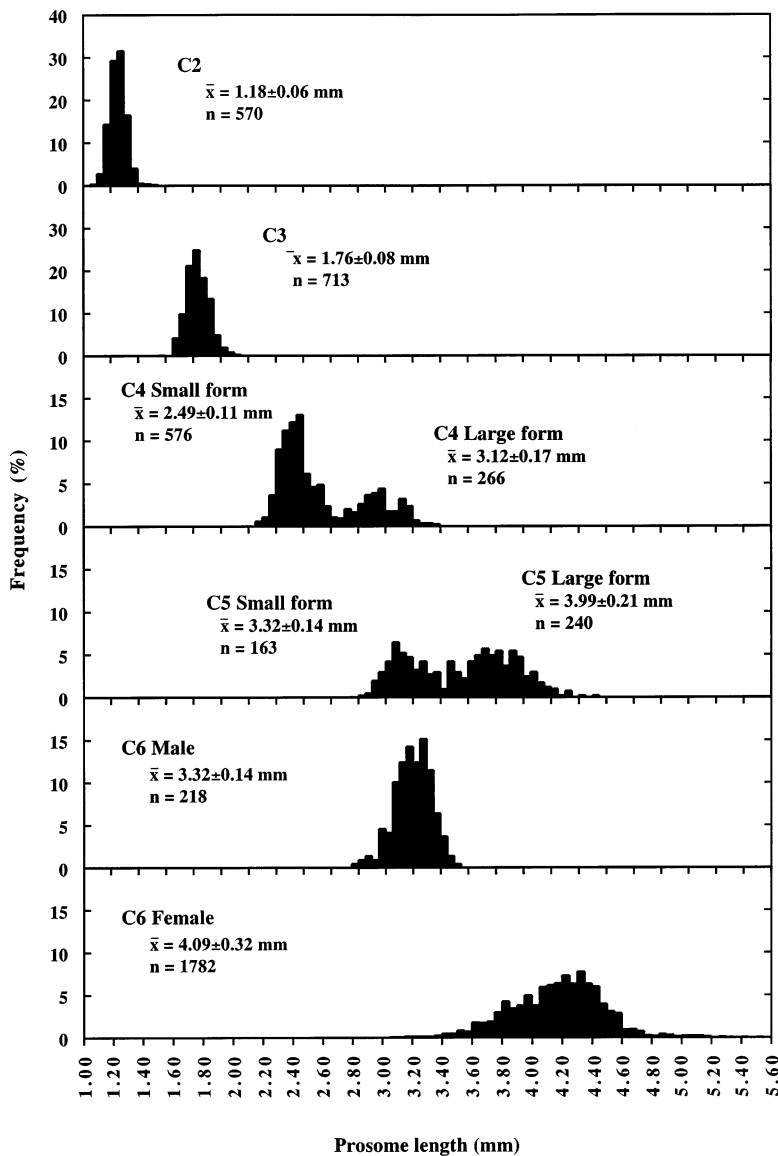


Fig. 7. *Neocalanus flemingeri*. Frequency-distribution of prosome length of each copepodite stage (C2 to C6) at Site H from September 1996 to October 1997. \bar{x} : annual mean, n: number of specimens measured

gins in November and spawning occurs in January. Thus, the life cycle of *N. flemingeri* is annual at Stn P.

The life cycle of *Neocalanus flemingeri* in the Japan Sea is somewhat different from that at Stn P because there appears to be 2 alternative diapause stages: C4 and C6 females. The latter type is the same as that observed in Stn P population (Miller & Clemons 1988). Miller & Terazaki (1989) hypothesized that the population diapausing as C4 during summer/winter might develop to C5, and then to C6 in the following year (i.e. biennial life cycle). Thus, there may be 2 *N. flemingeri* populations in the Japan Sea distinguished by annual versus biennial life cycles.

The life-cycle pattern of the main population of *Neocalanus flemingeri* at Site H in the Oyashio region is very similar to that at Stn P in terms of its ontogenetic vertical migration pattern, spawning timing, short-lived C6 males, and long-lived dormant C6 females (cf. Figs. 4 & 5). The only difference between our results and those of Miller & Clemons (1988) is the occurrence of a small overwintering population of C4 at Site H. Adopting the interpretation of Miller & Terazaki (1989) for the *N. flemingeri* population in the Japan Sea, this small C4 population overwintering at Site H may require 2 yr to complete its life cycle (Fig. 8).

Assuming that overwintering C4 and C6 females represent biennial and annual life cycles of *Neocalanus flemingeri*, respectively, the population structure data of other areas (Table 2) provide some insight into large-scale regional variations in the relative importance of the 2 life cycles of this copepod. Our observation of overwintering C4 in the Japan Sea but only C6 females in the eastern subarctic Pacific confirms the previous results of Miller & Terazaki (1989) and Miller & Clemons (1988), respectively. While overwintering C4 were not seen in the central subarctic Pacific, C4 were collected in the Okhotsk Sea and, to a small extent, in the western subarctic Pacific, including Site H. These results suggest that, for the subarctic Pacific and its marginal seas, a biennial life cycle is characteristic for a significant fraction of individuals from western Pacific populations. A biennial life cycle is not found among individuals from central and eastern Pacific populations. The differences in the life-cycle modes of *N. flemingeri* may be a response to east-west dissimilarities (see later subsection 'Regional body size variation'); i.e. overwintering C4 (biennial individuals) in the western region may represent those individuals that failed to encounter sufficient food and/or slower development in cooler conditions.

Sexual dimorphism

Among the C2 to C6 stages of *Neocalanus flemingeri*, the size distributions of C4 and C5 exhibited 2 modes, while all other stages showed only 1 mode (Fig. 7). Tsuda et al. (1999) interpreted the bimodal size distribution of C4 and C5 as a mixture of 2 populations with

Table 3. *Neocalanus flemingeri*. Prosome length (PL: mm) of C5 and C6 (males and females) in the subarctic North Pacific and its neighboring waters. Regional comparison was made for C6 females only against the means at Site H, OS97120 (the smallest mean) and HO97150 (the largest mean) (1-way ANOVA, Scheffé's *F*). Number of specimens in parenthesis. +, - : significantly greater or smaller, respectively, at $p < 0.05$ (+, -), $p < 0.01$ (++, --) and $p < 0.001$ (+++, ---). nd: no data

Area Station	Prosome length						C6 female	
	Mean \pm SD	(n)	Mean \pm SD	(n)	Mean \pm SD	(n)	Compared with Site H OS97120 HO97150	
NW Pacific								
Site H	3.67 \pm 0.38	(403)	3.32 \pm 0.14	(218)	4.09 \pm 0.32	(1782)		
19	3.75	(1)	nd		4.08 \pm 0.30	(211)	+++	---
HO96098	nd		nd		3.61 \pm 0.27	(100)	---	---
HO96107	nd		nd		3.81 \pm 0.36	(21)	---	---
NC Pacific								
OS97097	3.36 \pm 0.14	(244)	3.06 \pm 0.10	(85)	nd			
NE Pacific								
OS97130	nd		2.92 \pm 0.98	(6)	3.50 \pm 0.14	(72)	---	---
OS97120 (= Stn P)	nd		3.02 \pm 0.63	(10)	3.63 \pm 0.13	(102)	---	---
Bering Sea								
W303	nd		nd		3.96 \pm 0.23	(26)		---
Japan Sea								
C08	nd		nd		4.06 \pm 0.21	(16)	++	---
HO97103/HO97104	nd		nd		4.20 \pm 0.31	(100)	+++	---
I09	3.80	(1)	nd		4.00	(1)		
J07	3.70	(1)	nd		3.90	(1)		
Okhotsk Sea								
Ok30	nd		nd		4.47 \pm 0.45	(83)	+++	+++
HO97150	3.70	(2)	3.24 \pm 0.17	(10)	4.57 \pm 0.42	(154)	+++	+++

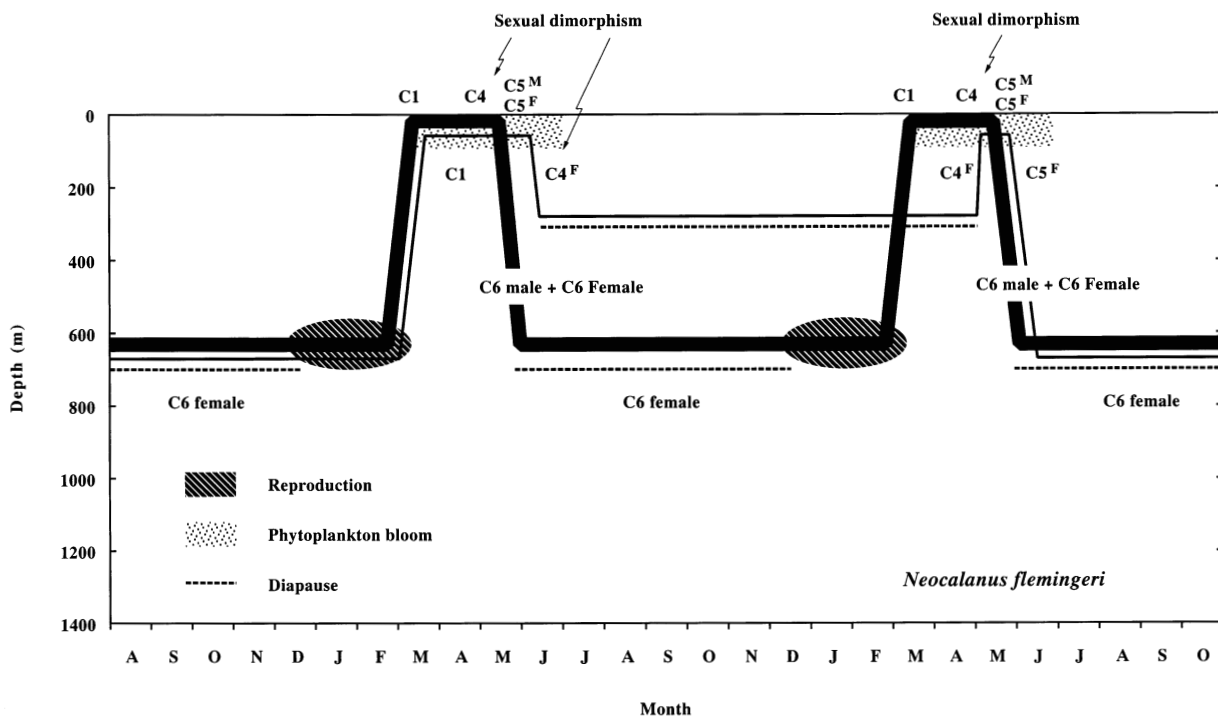


Fig. 8. *Neocalanus flemingeri*. Life cycle in Oyashio region. Annual life cycle trajectory is shown by thick line and biennial life cycle trajectory by thin line. Superscripts (M: male, F: female) denote expression of sexual dimorphism in C4 and C5

annual (small size, Oyashio population) and biennial (large size, Okhotsk Sea population) life cycles. Bimodal size modes of C6 females and males are less pronounced in Tsuda et al.'s data. Unfortunately the sampling depth (400 to 900 m) employed by Tsuda et al. was apparently not deep enough to collect the entire population of the C6 living >1000 m (cf. Fig. 5 of present study); therefore the size-distribution data of their C6 is subject to possible error. In fact, the size-frequency distributions of C6 females and males were unimodal in the present material collected down to 2000 m (Fig. 7).

As an alternative explanation for the observed bimodal size distribution of C4 and C5, we suggest sexual dimorphism within the same population. We hypothesize that the small-form C4 are sex-undetermined, and the small C5 are males, and the large form C4 and C5 are all females. To support this, the mean prosome length ratios of large to small specimens are 1.25:1 for C4, and 1.20:1 for C5, both of which are close to the prosome length ratio of females to males (1.23:1) of C6 adults. The mouth parts of adult *Neocalanus flemingeri* are reduced and nonfunctional (Miller 1988), implying that little dimensional change from pre-adult (C5) prosome length ratios would occur in adults. Comparing the 2 different size groups with the annual and biennial life cycles of *N. flemingeri* discussed above, 2 development scenarios of late-copepodite stages are considered possible, i.e. biennial life cycle: C3, large overwintering C4 females, large C5 females, C6 females; and an annual life cycle: C3, small C4 (sex-undeveloped), small male and large female C5, and male and female C6 (Fig. 8). In crustaceans, environmental factors such as feeding conditions, population density, temperatures, etc. are known to induce female characters (cf. Ginsburgur-Vogel & Charniaux-Cotton 1982), but mechanisms controlling the development of the C3 to large (female) or small (sex-undeveloped) C4 are presently unknown. In addition to Site H, we observed a bimodal size distribution of C5 in the central subarctic Pacific (small form: $\bar{x} = 3.15 \pm 0.09$ mm, $n = 298$; large form: $\bar{x} = 3.45 \pm 0.08$ mm, $n = 172$), but the number of the C4 and C5 specimens was too few at other stations to analyze (Table 2).

Bimodal body-length distributions have been reported for the C4 and C5 stages of *Calanus finmarchicus* and *C. helgolandicus* (Ussing 1938, Barnes & Barnes 1953, Marshall & Orr 1955, Woodhead & Riley 1957, 1959, Grigg et al. 1981, 1985, 1987), and explained for these species by sexual dimorphism (Woodhead & Riley 1957, 1959, Tande & Hopkins 1981, Grigg et al. 1987). According to Woodhead & Riley (1957, 1959), sexual size dimorphism in C5 of *C. finmarchicus* and *C. helgolandicus* appears not only as total body size but also as morphology of the first urosome segment. However, we could not find any morphological

differences between small and large size groups of C4 and C5 of *Neocalanus flemingeri* in the present study. According to Tande & Hopkins (1981) and Kosobokova (1998), the number of genital ducts is useful for separating males (single) from females (2) at C5 of *C. finmarchicus* and *C. glacialis*, but we did not examine this for *N. flemingeri* in this study.

Regional body-size variation

Body size of marine copepods is known to be influenced by water temperature and food availability, both in laboratory experiments (e.g. Corkett & McLaren 1978, Escribano & McLaren 1992) and from field-data analysis (e.g. Digby 1954, Deevey 1960). In general, lower temperature and higher food concentration produce larger body size in copepods. In the following discussion, we assumed that *Neocalanus flemingeri* is primarily a grazer, and used chl *a* concentration as an index of phytoplankton abundance.

Between-habitat comparisons of prosome length revealed that *Neocalanus flemingeri* from the Okhotsk Sea have the longest prosomes while those from the eastern (OS97120 and OS97130) and part of the western (HO96098) oceanic subarctic Pacific have the shortest (Table 3). Together with high chl *a* concentrations (max. 5 mg m^{-3} , Saitoh et al. 1996), the large body size of *N. flemingeri* in the Okhotsk Sea may be explained by the positive effect of lower habitat temperature due to the cold intermediate water, characterized by subzero temperature (Kitani & Shimazaki 1972 and present Fig. 3). In contrast, a warmer habitat temperature (Fig. 3) or the combined effects of a warm habitat temperature and low chl *a* (6 to 13°C , Miller et al. 1984, 0.1 to $0.6 \text{ mg chl } a \text{ m}^{-3}$, Welschmeyer et al. 1993) may explain the small body size of *N. flemingeri* in the oceanic gyre regions. In the Japan Sea, moderate chl *a* concentrations (max. 2 to 3 mg m^{-3} ; S. Kim et al. pers. comm.) and low deep-water temperatures ($<1^\circ\text{C}$; Fig. 3) are similar to those in the Okhotsk Sea, but the size of *N. flemingeri* in the Japan Sea is less than in the Okhotsk Sea, suggesting possible modification of the Japan Sea waters by the overlying Tsushima Warm Current. The intermediate body size of *N. flemingeri* in the western subarctic Pacific, including Site H and the Bering Sea, suggests that the combined effects of temperature and food phytoplankton conditions are similar in these 2 regions. In his original description of *N. flemingeri*, Miller (1988) noted regional variations in the size (C6 female), including specimens collected from Stn P, western subarctic Pacific, Japan Sea and Bering Sea. While Miller gave no interpretation for these regional variations, our data are in good agreement with his results (Table 3) for the same regions.

Three sympatric *Neocalanus* species occur at Site H in the Oyashio region. In addition to the present study on *N. flemingeri*, the life-cycle patterns of *N. cristatus* and *N. plumchrus* have also been evaluated (Kobari & Ikeda 1999a,b). These 3 species are similar in that they display large-scale ontogenetic migration (600 to 1000 m), spawn at depths below 250 m, and achieve rapid growth during their residence in the surface layer. However, in the Oyashio region there are some between-species differences in the timing of active development in the surface layer (order: *N. cristatus* > *N. flemingeri* > *N. plumchrus*), and the depth stratum during diapause (*N. cristatus* > *N. plumchrus* > *N. flemingeri*), thus facilitating niche separation in time and space (cf. Tsuda et al. 1999). Further, Mackas et al. (1993) observed a small-scale vertical partitioning of these 3 copepods during their copepodite growth season, i.e. *N. cristatus* resides below *N. flemingeri* and *N. plumchrus*. In addition, the present results illustrate that the life-cycle patterns of *N. flemingeri* are more complex than those of *N. cristatus* and *N. plumchrus* in that the former possibly displays sexual dimorphism in late-copepodite stages and comprises a mixture of individuals with annual and biennial life cycles.

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